

PHENOLOGICAL “RACES” OF THE *HESPERIA COLORADO* COMPLEX (HESPERIIDAE) ON THE WEST SLOPE OF THE CALIFORNIA SIERRA NEVADA

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ABSTRACT. On the west slope of the California Sierra Nevada, the subspecies *Hesperia colorado harpalus* (formerly generally known as *H. comma yosemite*) is univoltine, flying in midsummer at mid-elevations. In a number of sites, mostly on serpentine and other unusual soils, a variable but usually slightly darker *colorado* entity flies at similar elevations in September and October. The two are indistinguishable by male genitalia and thus far by mitochondrial DNA sequences. The autumn “race” is usually parapatric with the summer one and is sympatric with it at one known site. The hypothesis that the autumn “race” represents Sierran populations of subspecies *tildenii* of the North Coast Range is not consistent with our DNA data. Due to complete temporal isolation, the two “races” of *H. comma* are functioning as effective biological species.

Additional key words: serpentine, allochronic isolation, speciation, phylogeography, mitochondrial DNA.

Among the many mechanisms suggested for sympatric speciation, temporal (allochronic) isolation has been posited frequently, but rarely supported on further inquiry (Alexander and Bigelow 1960, Harrison and Bogdanowicz 1995, Huang et al. 2000 but see Feder et al. 1994). Allochronic isolation between close relatives is itself common enough, however, whether or not it is a cause of speciation (Coyne and Orr 2004). Two of the most compelling cases for allochronic speciation - sympatric or not - occur in North American Lycaenid butterflies of the genera *Apodemia* (Pratt and Ballmer 1991) and *Euphilotes* (Pratt 1994, Pratt and Emmel 1998). In both genera, allochronic “races” or “biotypes” have arisen within morphospecies, reflecting adaptation to specific hosts in the large Polygonaceous genus *Eriogonum*. The feeding biology of these insects requires close tracking of host flowering phenology, which varies widely among species. The “races” are frequently sympatric, even over wide areas, but since they are completely isolated they are functioning as effective species. They may have diverged too recently to show significant differentiation at the molecular level (Peterson 1995). Allochrony is also a factor in incipient speciation by “host races” in the Cupressaceous-feeding Lycaenid genus *Mitoura* (Nice and Shapiro 2001). In this case also, butterfly phenology is most likely a function of host phenology (i.e. the availability of new growth), as host association is a better predictor than altitude of adult flight period in areas where races overlap geographically (though the relationship between host phenology and the preference and performance of butterflies is complex, see Forister

2005). We here report a case of sympatric, allochronic “races” in the *Hesperia colorado* (Scudder) complex (Hesperiidae) in the Sierra Nevada of California, with no obvious adaptive relation to host phenology.

ECOGEOGRAPHY OF THE “RACES”

These skippers belong to a circumpolar (Holarctic) complex historically called collectively *Hesperia comma* (L.). Recent authors have split off the Nearctic members of this complex, except those of the far Northwest, as a separate species, *H. colorado* (Scudder). The complex was studied phylogeographically by Forister, Fordyce and Shapiro (2004), whose findings broadly support this division. Within the Nearctic range (excluding the far Northwest), these authors found the maximum geographic structure for the mitochondrial gene (COII) they studied to be in California, with two major genetic discontinuities centered around the Sierra Nevada and Transverse Ranges.

The subspecific nomenclature of the populations at issue is very confused. Historically, east-slope Sierra Nevada populations were placed in subspecies *harpalus* (W.H. Edwards) and west-slope ones, which are phenotypically quite different, in subspecies *yosemite* Leussler. Scott (1998) found that the conventional usages were incorrect and that these two names are in fact synonyms and *harpalus* is the correct name for the west-slope entity, while the correct name of the east-slope one is *H. c. idaho* (W.H. Edwards). We review this taxonomy because in using the subspecies as redefined by Scott in this paper, we risk causing confusion in the context of virtually all prior

publications on the group. The name applied to the Inner North Coast Range subspecies (*tildeni* H.A. Freeman) is unaffected.

Both west-slope *harpalus* and east-slope *idaho* are univoltine (as is the entire complex) and fly in early-to-midsummer. Coast Range *tildeni* fly later, typically from August through October. In the early 1970s one of us (AMS) discovered a population near 1500m in Nevada County, CA on the Sierran west slope that flew only in September and October. AMS continued to monitor this population annually. In 1988 it was included in a permanent monitoring site on his altitudinal transect across California and has thus been visited approximately biweekly except in winter since then. Its autumnal flight period has remained constant throughout. It is limited to a serpentine barren with sparse vegetation, much bare rock and only one nectar source, a distinctive dwarfed ecotype of rabbitbrush, *Chrysothamnus nauseosus* (Pallas) Britton (Asteraceae), during its flight season.

Populations of summer-flying *H. c. harpalus* occur in the same canyon at 850m and 1525m on metasedimentary substrates (phyllite and complex schists) at distances of 4 and 11 km respectively, as well as at 2100m on an andesitic mudflow and granodiorite, 40.5 km away. The phenology of these three

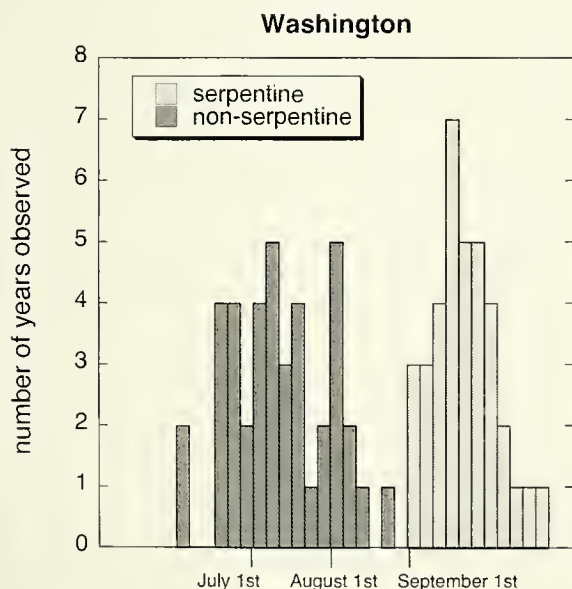


FIG. 1. Histogram showing the phenology of the two *H. colorado* races at Washington (Nevada Co.) since 1988. Vertical bars correspond to five day increments (the beginning of July, August, and September are shown for reference). For example, there were five years in which non-serpentine *H. colorado* individuals were observed at this site during the first five days of August.

populations (identified as Washington, Lang Crossing, and Donner Pass) is compared with the autumnal one (identified as Washington Serpentine) in Figs. 1 and 2. The serpentine population (Washington serpentine) is later-flying than the 850m Washington population

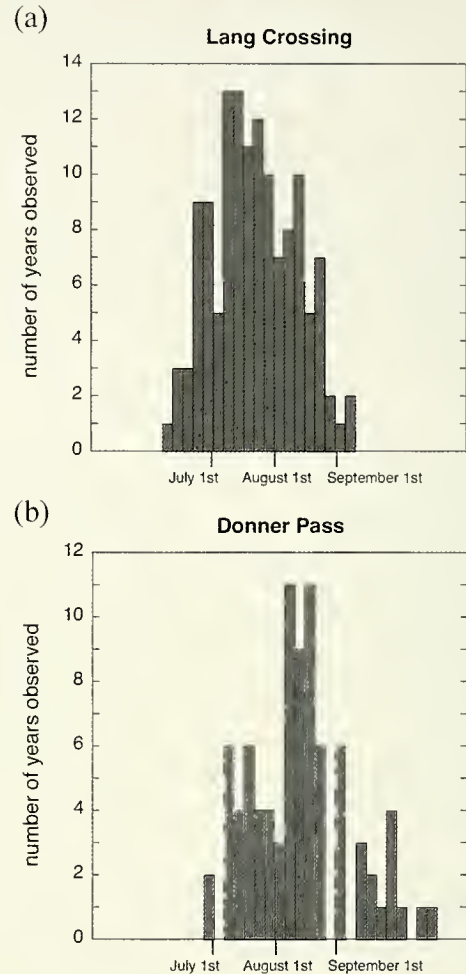


FIG. 2. (a) Histogram showing the number of times that *H. colorado* individuals have been observed throughout the year at Lang Crossing (Nevada Co.) since 1974, and (b) at Donner Pass (Nevada Co.) since 1973. As in Fig. 1, time on the x-axis is expressed in vertical bars indicating observations made within five day intervals.

(there is no overlap), and only overlaps with the 1525m Lang Crossing population by a few days. Individuals at the 2100m Donner Pass population have been observed as late into the fall as at the serpentine population, but this is clearly a phenological effect of high-elevation conditions (there is only one brood at Donner Pass).

Once alerted to the presence of an autumnal race on unusual soils, AMS and his associates began looking for additional autumn-flying populations, primarily on serpentine. Gervais and Shapiro (1999) reviewed the

distributions of edaphic-endemic butterflies in the Sierra Nevada, including the autumn "race" of *H. colorado* (there called *comma*). They reported populations on serpentine and gabbro soils in Nevada, Placer and El Dorado Counties on the west slope, as well as one on limestone in Calaveras County and one on an undetermined substrate in Mariposa County (reported to us by Oakley Shields). There are undoubtedly more populations to be found, and the association with unusual soils may be more apparent than real since we mainly looked for them on such substrates. The populations we identified all appear to be parapatric with summer *harpalus* on "normal" substrates nearby, except one (Drum Powerhouse Road, Placer County, in the Bear River drainage) in which

they are actually sympatric, but allochronic, in an area where serpentine and metasedimentary rocks are intimately interdigitated, and some of the serpentine is unusually mesic.

We have been unable to find any male genitalic differences between these "races" (C.D. MacNeill, pers. comm.). The phenotypes of the autumn "race" are about as variable as summer *harpalus*, though on average slightly darker with a more defined ventral hind wing pattern. Fig. 3 illustrates the phenotypes. We have not identified any consistent character in either sex which can be used to identify flight date correctly. (It should be noted that some individuals of the autumn "race" rather closely resemble the apparent hybrid swarm between east- and west-slope subspecies in the

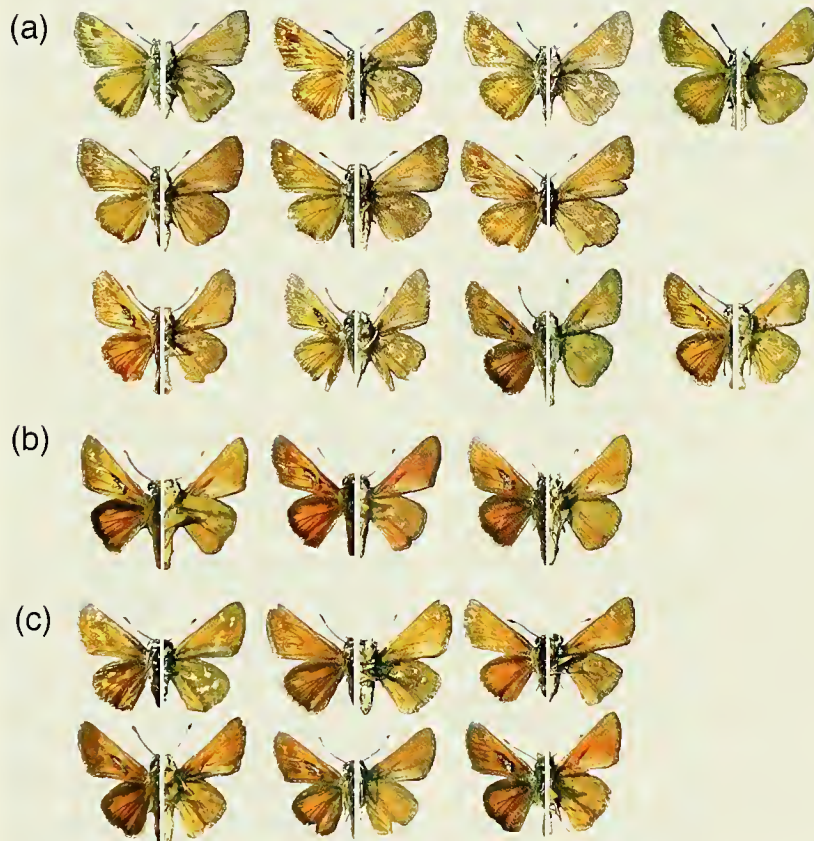


FIG. 3. Photographs of *H. colorado* specimens (showing left dorsal and ventral views): (a) seven females and four males, serpentine "race" from Washington, (b) three males, non-serpentine "race" from Washington, (c) three males and three females, from Lang Crossing.

Feather River Canyon farther north in the Sierra. These animals fly very early, in May and June.) Molecular-genetic evidence bearing on the identity of the autumn "races" is discussed below.

DISCUSSION

An endemic late-season serpentine subspecies of *Hesperia colorado*, described from the Siskiyou mountains of far northern California, was named *mattoonorum* by McGuire (1998). This entity is darker on average than nearby non-serpentine populations, but is also variable. Those nearby populations are extremely variable and confusing. Scott (1998) synonymized the usual name applied to them, *oregonia* (W.H. Edwards), with *harpalus* as well. In our judgment his fixation of the type locality of *oregonia* as "Sierra Nevada Mts., west of Carson City," is unjustified by the historical and biological facts. In any case, Shapiro, Palm and Weislo (1991) recorded *tildeni*-type foothill *H. colorado* in the Trinity Alps from 7-29 August; "light" *oregonia* (from rain-shadow areas) from 16 August - 20 September, and "dark" *oregonia* (from wetter areas) from 12 July through 25 September. The very long type series of *mattoonorum* was collected in September. Shapiro (1991) illustrated a hypervariable population series from a serpentine site in the nearby Trinity Divide, collected 5 September. Because of the very extended flight seasons of far northern California *colorado*, it is difficult to assess the significance of the late flight season of *mattoonorum*. No *mattoonorum* were available for molecular-genetic study, but several specimens from the upper foothills of the Trinity Alps above French Gulch were used.

When Gervais and Shapiro (1999) discussed the geography of edaphic-endemic Sierran butterflies, they proposed the hypothesis that the autumn "races" of *H. colorado* were actually populations of the late-season-flying Inner Coast Range subspecies *tildeni*, signifying a double invasion of the Sierra. This was suggested by the fact that most of the edaphic-endemic entities they found were much more widespread in the Coast Range (and had been largely or entirely overlooked in the Sierra) and that their ranges in the Sierra, including autumn *colorado*, were largely concordant, suggesting a common history.

Forister, Fordyce and Shapiro (2004) found for a portion of the COII mitochondrial gene, coast Range *tildeni* possessed a unique haplotype (D) not found in far-northern California and Oregon or in the Sierra Nevada (see Fig. 1 in Forister *et al.* (2004) for the distribution of haplotypes in the Western United States). The Sierran east and west slopes shared no haplotypes, except in the thoroughly mixed Feather

River hybrid population. They sequenced COII from 5 Washington serpentine animals (Nevada County), all of which were haplotype A, the most common haplotype on the Sierran west slope and in Oregon. Haplotype A does not occur in Coast Range *tildeni*, and is two mutational steps removed from the *tildeni* haplotype D in the statistical parsimony network described by Forister *et al.* (2004). Three Lang Crossing *harpalus* were A, two B; one summer *harpalus* from Drum Powerhouse Road was A (B is one mutational step from A). The serpentine series seems unusually invariant, but cannot be distinguished from nearby summer *harpalus*. On the other hand, the hypothesis that it is really *tildeni* is not supported by our data since haplotype D was not found. Two individuals from the foothills of the Trinity Alps were haplotype B, one I (B is connected to I by one mutational event, and I is two steps removed from A).

Forister *et al.* (2004) found no geographically patterned variation for the nuclear gene *wingless* in North America south of British Columbia. We are thus unable at this time to identify any genetic discontinuity between summer *harpalus* and the autumn "race" in the Sierra Nevada. It is possible that a survey of nuclear variation encompassing a larger portion of the genome would reveal such differences, but we have been unwilling to sample these mostly very small populations to the extent needed for statistical rigor.

Unlike the *Eriogonum*-feeding Lycaenids with phenological "races," there is no obvious connection between the seasonality of these *Hesperia* and their presumed host plants, perennial bunchgrasses. We do not know the hosts used by them at any of the sites mentioned except Lang Crossing, where summer *harpalus* routinely uses the naturalized European grass *Anthoxanthum odoratum* L. (Poaceae). This grass does not occur at any of our other sites in the region. *Hesperia colorado* overwinters as an egg, and larvae feed on young growth in the spring. The flight season of the adults thus appears decoupled from any need to match host phenology, although it could be related to the ability of the eggs to tolerate late-summer desiccation prior to the onset of winter. Until appropriate experiments are done, we will be unable to state whether the autumn "races" are genetically programmed to emerge at that season or are somehow induced physiologically to do so as a result of the nutritional properties of their hosts — which in turn could be affected by occurrence on serpentine vs. non-serpentine substrates. We do not know if the northern entity *mattoonorum* is in any way connected with the Sierran serpentine populations, or whether autumn "races" in the Sierra are all derived from a single

ancestor or have arisen repeatedly in various locations from local summer *harpalus*, in the manner of many plant ecotypes which are generated over and over again. Our nearest sample to *mattoonorum*, from French Gulch (Trinity County), is not that entity and is thus not informative.

CONCLUSIONS

1. Local autumn-flying "races" of *Hesperia colorado* occur within the range of summer-flying subspecies *harpalus* on the west slope of the Sierra Nevada. Most of these known to date are on serpentine or other unusual soils.

2. These autumn "races" average a little darker than nearby *harpalus* but have no definitive wing, genitalic, or molecular characters to allow them to be identified without collection dates.

3. Despite similar seasonality and biogeographic arguments, molecular phylogeography has not supported the hypothesis that the Sierran autumn "races" are actually the Inner Coast Range subspecies *tildeni*.

4. Further study is needed to distinguish between genetic and environmental/physiological factors as determinants of the aberrant phenology of these "races."

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